Dead wood matters – a snapshot in time of one hectare of the floor of a *Eucalyptus obliqua* forest in Southern Tasmania

Genevieve M. Gates & David A. Ratkowsky
Tasmanian Institute of Agriculture, University of Tasmania, Hobart, Tas. 7001
Genevieve.Gates@utas.edu.au & D.Ratkowsky@utas.edu.au

Abstract

Wildfires in wet eucalypt forests, depending on their intensity and frequency, generate dead wood of varying sizes and in many different stages of decay. Windthrow events also contribute to large dead wood lying on the forest floor. In this study, CWD (coarse woody debris), defined as dead wood at least 10 cm diameter and 1 m long, and dead standing trees (stags) were measured and their attributes recorded in four 50 x 50 m plots within ca. 1 km of each other but with differing wildfire histories in a tall, wet, native *Eucalyptus obliqua* forest in southern Tasmania. Maps of the CWD and stags for each of the four plots were drawn and show substantial differences between the four plots. Information from four other surveys of CWD in the same forest type provided a degree of replication to this study. Comparisons among the studies showed that the CWD volumes in plots of similar age since wildfire were very variable and most likely reflect the chance location of large fallen eucalypts in the plots. This suggests that more surveys such as these are needed to determine the average CWD volumes in these forests. Knowledge of these volumes is required to develop forest dynamics models to predict the amount of CWD that would be present as a result of various disturbance and management scenarios. Dead wood is seen to be an important resource in these tall, wet forests, harbouring biodiversity and storing carbon. The challenge for the Tasmanian forest industry in the future may involve the development of energy-efficient methods so that mixed forests, which store carbon to a greater extent than pure eucalypt forest or pure rainforest, can produce wood products such as furniture, floors, veneers and musical instruments and do it in a manner that minimises carbon loss, to make no net contribution to global warming.

Introduction and background

Dead wood in forest ecosystems has been recognised for some time as being important in providing a range of ecological niches that maintains many specialist wood-dwelling species such as beetles, slime moulds and fungi, and houses hollow-dependent birds and mammals, as well as serving as a temporary sink for forest carbon and other elements (e.g. Harmon *et al.* 1986; Grove *et al.* 2002; Stokland & Sippola 2004; Wu *et al.* 2005). In a forest ecosystem, dead wood consists of all dead natural structures of woody plant origin, which includes dead roots, stumps, fallen tree trunks, branches, twigs, and standing dead trees (stags). Natural mortality of a tree occurs due to ageing and suppression caused by competition as the stand develops after disturbance. The disturbance may be natural (e.g. windthrow, wildfire, earthquakes) or caused by humans wanting to harvest timber, pulpwood and firewood. The quantity of dead wood input into the ecosystem following any of these disturbances may be large and immediate as with a catastrophic event or a more gradual process in time, which may be seasonal, annual or long-term (Harmon *et al.* 1986). Spatial input may be within stands or across landscapes and catchments. However, most inputs of dead wood occur at the local scale (e.g. within one tree length of the source). Knowledge of the natural dynamics of dead wood provides important baseline data that can be used for developing and evaluating strategies to lessen the pressure of human-caused disturbance on wood-inhabiting organisms (Jonsson 2000). It is customary to divide dead wood into coarse woody debris (CWD) and fine woody debris (FWD), but the dividing line between these categories depends upon the investigator. In the present study, CWD was defined to be all pieces of dead wood ≥10 cm diameter and ≥1 m length, a modification of the recommendation of Harmon & Sexton (1996). This definition of CWD included stumps, suspended pieces of wood, and shards (shattered pieces of larger logs) as well as fallen trunks and branches on the forest floor.

In Australian eucalypt-dominated forests, fire is the major cause of large-scale natural disturbance. Wildfires vary in type (Luke & McArthur 1978), intensity (Gill 1997), size, frequency and homogeneity (Ashton 1981), resulting in differing starting points for new stand development. There is generally a lack of knowledge regarding the log accumulation rate, i.e. the time frame over which trees fall and become logs on the forest floor, the rates of log decay and how these rates differ between managed and unmanaged forests in Australia (Lindenmayer *et al.* 2002). This lack of knowledge makes it difficult to determine how long it may take logged areas to accumulate volumes of CWD equivalent to pre-harvesting levels and to establish silvicultural regimes that ensure that forests are sustainably managed (Lindenmayer *et al.* 2002).

In the commercially important wet lowland eucalypt forests of southern

Tasmania, mature trees of *Eucalyptus obliqua* (stringybark) frequently attain a height of over 70 m (Kirkpatrick & Backhouse 1981), enabling these forests to produce a wood volume per hectare which is amongst the highest produced by any forest in the world (Woldendorp & Keenan 2005). Mortality in these forests results not only from catastrophic fire, but also in developing stands through natural selection and suppression of smaller, weaker individuals. These smaller stems are commonly killed by insect and fungal attack or a combination of these factors and produce smaller diameter dead wood. Smaller diameter CWD may also accumulate from branch wood that has fallen from the canopy. In these forests, wildfires that do not result in stand replacement occur more frequently than stand-replacing wildfires (Alcorn *et al.* 2001; Turner *et al.* 2009). This has resulted in a mosaic of multi-aged forest stands of largely unknown dead wood complexity.

We believe that dead wood matters. As recognised by Yee *et al.* (2001), Grove (2009b) and Wardlaw *et al.* (2009), large diameter decaying logs, a characteristic feature of unmanaged wet sclerophyll forests in Tasmania, are an extremely valuable biological resource, belying the attitude that they are just "waste wood" and therefore suitable for little else other than to be burnt to generate electricity. Grove (2009a) summarised the first decade of research at the Warra LTER into how the option for generating electricity from harvest residues might impact upon the biodiversity associated with CWD, originally mainly saproxylic beetles, but later encompassing wood-inhabiting fungi, macrofungi in general, bryophytes, and other insects and invertebrates besides beetles. Wet eucalypt forest has recently been estimated to have an average carbon density of 378 tonnes C/ha, which occurs as the forests transition to mixed forest (eucalypt overstorey and rainforest understorey) (Moroni *et al.* 2017). If left undisturbed, these mixed forests eventually transition to rainforest, when the forests can lose more than half their bole wood volume and biomass as a consequence of rainforest trees being smaller than eucalypts, with the majority of the lost wood ending up as CWD. Maximising carbon stocks at the landscape level may require periodic disturbance in the form of harvesting for wood products such as furniture, boats, housing, veneers, fence posts, musical instruments and a whole host of other utilitarian and aesthetically pleasing products. Grove (2009a) coined a new word, "deadwoodology", and he recognised that the full implications for forestry of the growing awareness of carbon budgets are still to be discovered. He concluded that the study of dead wood was certain to play a part in understanding the role of carbon in the environment.

Volumes of CWD and numbers of stags are two of the attributes used to measure stand structure and which provide quantitative evidence of habitat that can be used in biodiversity studies (McElhinny *et al.* 2005). The volume input, connectivity (in space) and continuity (in time) of CWD are important considerations in sustainable forest management (Grove *et al.* 2002). In the present study, we recorded and mapped the dead wood present in a tall wet *E. obliqua* forest in southern Tasmania containing stands resulting from different wildfire events and we compared the CWD volumes from this snapshot in time with available information from four other studies (Woldendorp *et al.* 2004; Yee 2005; Sohn 2007; Thauvin *et al.* 2010) carried out in the same forest type.

Methods

Study area

The study area was at the Warra Long Term Ecological Research (LTER) site in the Huon River valley, southern Tasmania, Australia, where four 50 x 50 m plots were established in March–April 2006 along the 'Bird Track' (see Figure 1; the track received its name from the fact that it was used for an earlier study of the birds of this area). The plots were all within ca. 1 km of each other (ca. lat./long. S 43º 06', E 146º 39') and had similar south-facing aspect, altitude, rainfall and temperature, but differed in their wildfire histories. Documented accounts, maps of fire history and fire scars on *E. obliqua* trees were used to determine age since fire (Turner *et al.* 2007). Time since wildfire for each of the four plots was estimated, respectively, to be at least 200 years (named 'Old growth'), 108 years (named '1898' as it was burnt by a fire in 1898, but later it was discovered that a part of it had also been burnt by a fire in 1934), 72 years (named '1934', burnt by a fire in 1934) and 108 years/72 years (named '1898/1934', burnt by fires in 1898 and in 1934). Plot names are used for convenience but also reflect, at least to some extent, the disturbance history of the plot.

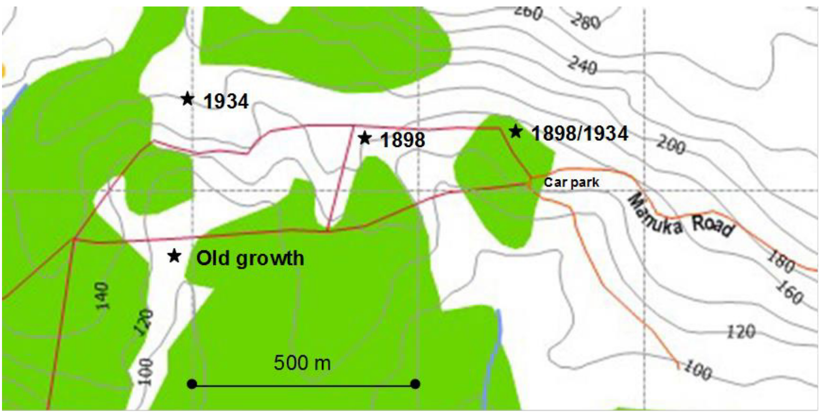

Figure 1. Location of the four plots used in this study along the 'Bird Track', Warra LTER site.

Each 50 x 50 m plot was established in the following way. Star pickets were placed at 10 m intervals along the outer boundaries of the two opposite sides of the plot. Twine was strung from the star pickets across the plot and fibreglass rods were placed at 10 m intervals along the twine to divide the plot into 25 subplots each measuring 10 x 10 m. This facilitated mapping of the CWD and stags.

CWD mapping

CWD originating from all woody perennial species was included in the study. CWD was consecutively numbered within each subplot. If a piece of CWD traversed two or more subplots, its length was measured to the boundary of the subplot and it was renumbered as a separate piece of CWD in the adjacent plot. The position, orientation and attributes (see below) of every piece of CWD in each subplot were recorded for each of the four sites. This information was transcribed onto large sheets of graph paper (laminated to make them usable in wet weather) marked with plots and subplots at a scale of 1 mm equal to 10 cm. The following attributes of each piece of CWD were recorded: 1) CWD length (cm); 2) CWD diameter (cm) measured at the mid-point of the piece of CWD; 3) CWD decay class (using a scale from 1 to 5 with intervals of 0.5; see Table 1a); and 4) percentage bryophyte cover on each piece of CWD (a visual score of 0–100%). Stumps were measured for decay class, height and mid-diameter (i.e. the diameter mid-way between the ground and top of stump).

The system of decay classes used in the Northern Hemisphere for their dead wood species had to be modified to accommodate the different wood species found in Tasmania and their differing rates of decay. In particular, the decay classification for CWD used here (Table 1a) was devised to try to overcome the problems associated with the unevenness of the interval between decay classes 3 and 4. If a piece of CWD had more than one decay class, an average was taken (after Pyle & Brown 1999). For analysis, CWD was placed into the following diameter classes: ≤15 cm, 15–30 cm, 30–60 cm, 60–90 cm, 90–120 cm, 120–150 cm, >150 cm. These classes were deemed to be most useful in forest management by Forestry Tasmania (Simon Grove, pers. comm.; Yee 2005). During analysis, other variables were derived from length and diameter by calculation, viz. volume and surface area, assuming that the shape of a piece of CWD approximated a cylinder. For stumps, height replaced length.

Stag mapping

Stags were recorded in a similar way to CWD, except 1) height was used in place of length; 2) diameter was measured at breast height; 3) decay was assessed using a modified system to that used for CWD, see Table 1b, following Cline *et al.* (1980), Spies *et al.* (1988) and Motta *et al.* (2006).

Statistical analyses

The statistical analyses were mainly descriptive, producing summary statistics. As the CWD was measured within each subplot, this enabled certain statistics such as minimum and maximum subplot volumes to be calculated for each plot, and also proved useful in a subsequent survey of the macrofungi growing on wood (see Gates *et al*. 2011). At the plot level, the results presented here mostly used composite pieces of CWD, obtained by concatenating the information on pieces of CWD that crossed subplot boundaries. Graphical methods involved one variable at a time for percentage of pieces of CWD in each decay class and percentage bryophyte cover on CWD. Stags were examined by calculating the number of stags and their diameters in each plot and by recording the number of stags in each percentage bryophyte cover class.

Table 1. CWD and stag decay classification to accommodate *E. obliqua* and other tree species. (a) CWD, (b) Stags.

Decay class	**(a) CWD: Characteristics for classifying CWD**
1	CWD freshly downed, entire, cylindrical, wood hard, sound, bark intact, no sign of internal decay or external macrofungal fruit bodies.
1.5	Wood has been lying on the ground for some time, cracks appearing in bark.
2	CWD remaining solid, losing some bark, some macrofungal fruit bodies appearing, bryophyte cover sparse.
2.5	CWD with many macrofungal fruit bodies, but exhibiting no sign of softening. Category included to accommodate *Pomaderris apetala*.
3	CWD retaining round shape, bark may be present, bryophyte cover present but variable, some degree of heart rot, still quite firm on the outer surface, many external macrofungal fruit bodies present in season.
3.5	CWD beginning to flatten, becoming softer, often with seedling trees, wood-inhabiting macrofungal genera being commonplace, bryophyte cover substantial. Roots from nursery trees making their first appearance.
4	CWD half its original diameter, often with only the sides remaining but still recognizable as a log or a log that may be prolifically interspersed with roots from nursery trees of considerable size.
4.5	CWD disintegrating into splinters and losing outline.
5	CWD reduced to a pile of humus, still with very small wood fragments present, outline just visible, mound-like appearance or a 'cage' of roots from a nursery log with some woody humus remaining.

Decay class	**(b) Stags: Characteristics for classifying stags**
1	Stag limbs and branches all present; 100% bark present.
2	Stag has some loss of limbs and bark but is sound at base.
3	Stag distinctly rotten at base; in *E. obliqua* the bark can still be intact at this stage.
4	Stag still standing with outer bark intact but obviously very decayed inside. This category is for *Nothofagus* stags.
5	Stag reduced to a thin central core, no outer wood but still standing. This category is for *Nothofagus* stags.

Results

CWD maps

Maps showing the positions of CWD in each plot are given in Figure 2. Of the total of 814 pieces of composite CWD, 227 pieces were in 'Old growth', 138 in '1898', 212 in '1934' and 237 in '1898/1934'. The relative sparseness of pieces of CWD in '1898' (Figure 2b) compared with the other plots is readily observable.

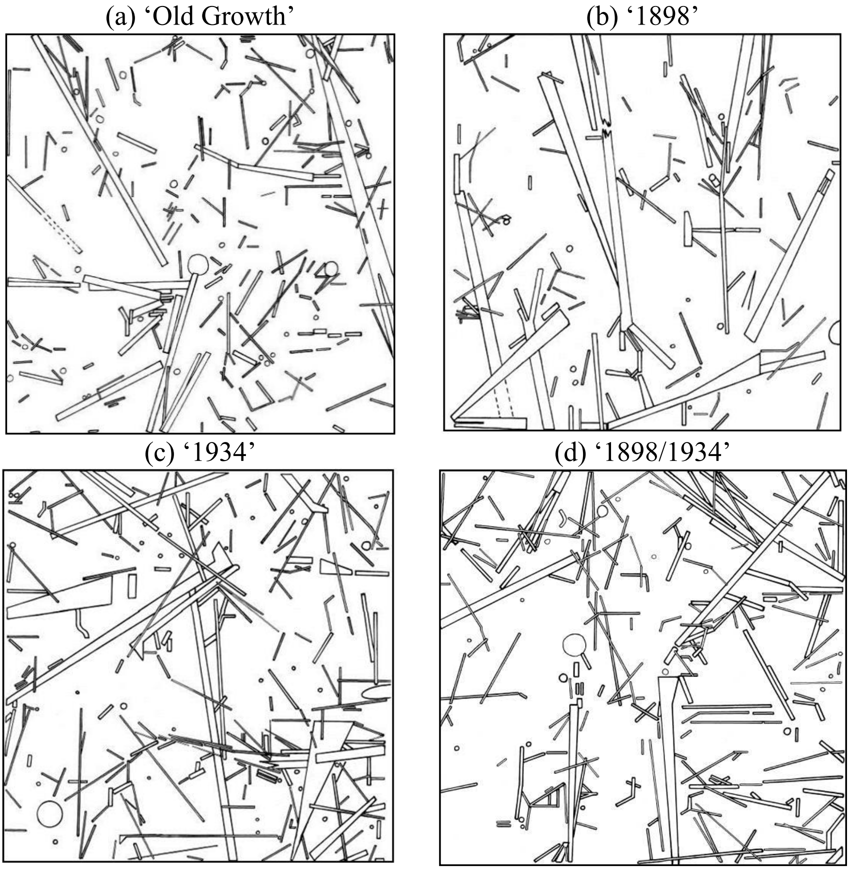

Figure 2. Maps of the CWD in the four plots at the Warra 'Bird Track'. Stags are represented by circles. Large diameter and long CWD are drawn to scale in these 50 x 50 m plots (very small CWD may be represented as larger than their true size at this scale).

CWD attributes versus diameter class

Figure 3 displays the percentages of pieces of CWD in each diameter class for each plot separately and for all plots combined. The greatest discrepancy occurs in the diameter class 15<D≤30 cm between 'Old growth' (109 pieces of CWD) and 1898 (39 pieces of CWD in that class) or, in percentage terms, 48% vs. 28.3%. 'Old growth' and '1934' each have their maximum in the 15<D≤30 cm diameter class, whereas for '1898' and '1898/1934', their maximum occurs for the smallest diameter class (D≤15 cm) and progressively declines with increasing diameter class. In 'Old growth', almost all of the CWD was in low diameter classes, with only 7.1% of its pieces of CWD having a diameter ≥60 cm, contrasting with '1898' which had 15.9% of its pieces of CWD in the large diameter classes of 60 cm or more.

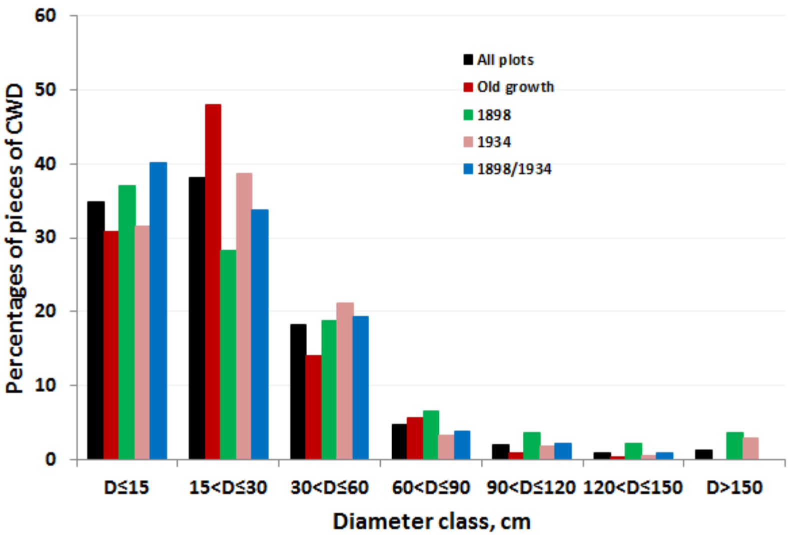

Figure 3. Percentage of pieces of CWD in each diameter class for each plot separately and for all plots combined. The percentages add up to 100% within a plot. The greatest discrepancy among plots occurs in the 15<D≤30 cm diameter class, where the contrast between the 'Old growth' and the '1898' plots is noteworthy.

CWD attributes versus decay class

Most of the 814 pieces of composite CWD within the four plots fell in the middle decay classes (DC3 and DC3.5), with 522 pieces of CWD (64.1%) in these combined classes (Figure 4). 'Old growth' had a very small percentage of CWD in the lower decay classes (DC≤2.5) compared with younger plots, but this was compensated for in the higher decay classes (DC≥4). Bryophyte cover tends to increase steadily as decay class increases in units of 0.5 from DC1–DC5 in all plots combined (Figure 5). Slightly deviating from the overall trend is '1934', which reaches a plateau at a percentage bryophyte cover of ca. 50% in the higher decay classes.

CWD and stag volumes

For each plot separately, minimum, median and maximum CWD subplot volumes are given in Table 2, which also gives the total plot volumes. Based on total volume (m^3/ha) of CWD present, '1898' had more than twice the volume of '1898/1934', whereas for stags (Table 3), '1898' had the lowest volume.

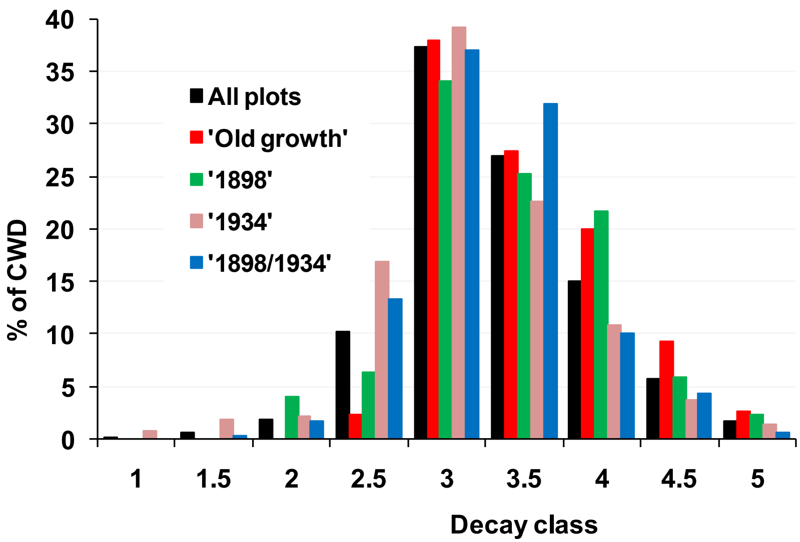

Figure 4. Percentage of pieces of CWD in each decay class for each plot separately and for all plots combined. The percentages add up to 100% within a plot. Noteworthy is the paucity or lack of 'Old growth' CWD in the low decay classes.

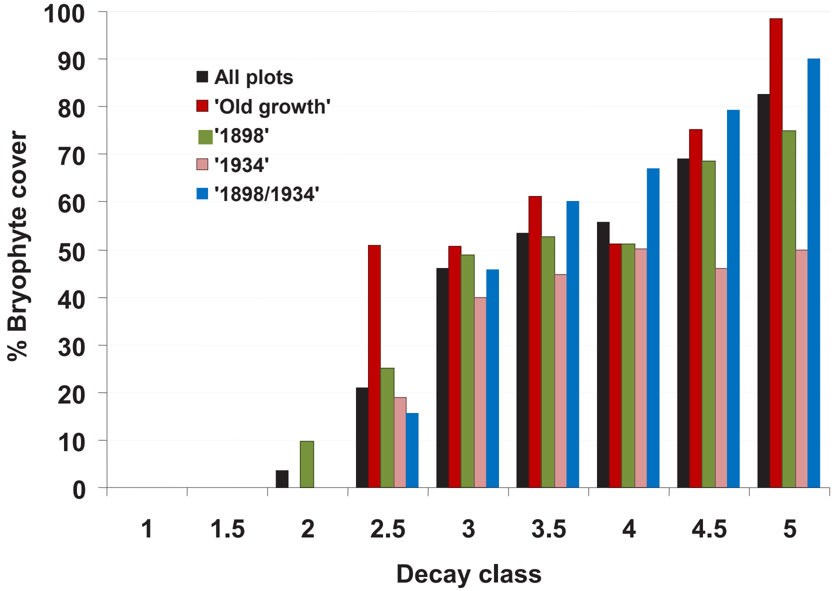

Figure 5. Average percentage bryophyte cover on CWD in each decay class for each plot separately and for all plots combined. The general trend is for an increase of bryophyte cover with increasing decay class, the exception being the '1934' plot which peaks at DC=4 and then levels off.

Table 2. Subplot minimum, median and maximum volume of CWD (in the 25 subplots) for each of the plots 'Old growth', '1898', '1934' and '1898/1934', and the total volume and total volume/ha for the same plots.

	'OG'	**'1898'**	**'1934'**	**'1898/1934'**
Minimum volume m^3	0.63	0.43	0.26	0.26
Median volume m^3	3.72	13.53	9.68	6.71
Maximum volume m^3	34.4	45.9	37.1	21.1
Total volume m^3	209.5	361.7	272.7	175.3
Total volume m^3/ha	**838**	**1447**	**1091**	**701**

Stag numbers and attributes

The '1934' plot had the greatest number of stags, closely followed by 'Old growth', while '1898' had the least number (Table 3). Although '1934' had 34 stags, all but one of them was of small diameter (Figure 6), so that the stags of that plot had the smallest average diameter of the four plots (Table 3). In contrast, although '1898/1934' had only 20 stags, that plot had the highest average diameter due to four stags of large diameter, each >100 cm (Figure 6). 'Old growth' had two large diameter stags (Figure 6), giving it the second largest average diameter (Table 3). With respect to species composition, there is a sharp contrast between the younger stands, '1934' and '1898/1934', which had 16 and 12 *E. obliqua* stags, respectively, and the mature forests, '1898' and 'Old growth', which had only one *E. obliqua* stag each (Table 3). The identifiable stags in 'Old growth' are mainly of *Nothofagus cunninghamii* (myrtle beech), *Atherosperma moschatum* (sassafras) and *Acacia melanoxylon* (blackwood), all of which are typical rainforest species.

The number of stags as a function of bryophyte cover class and plot is shown in Figure 7. Increasing bryophyte cover is associated with increasing age of plot, with few stags in '1934' and '1898/1934' having bryophyte cover of 25% or more.

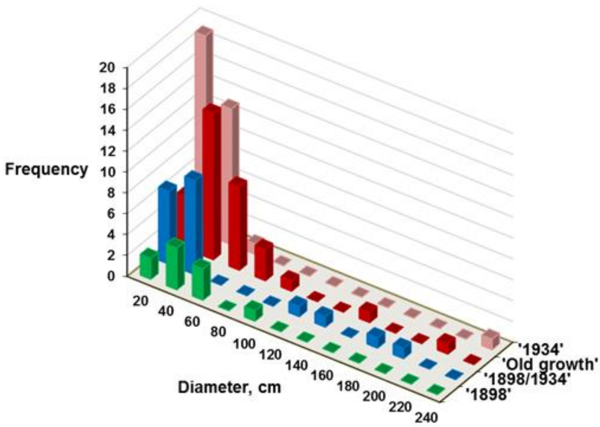

Figure 6. Diameter distribution of stags in the four plots at the Warra 'Bird Track'. Although plots '1934' and 'Old growth' had almost the same number of stags (34 vs. 33), those for '1934' were mostly concentrated in the two lowest diameter classes (D≤40 cm), whereas 'Old growth' had more stags in the higher diameter classes. Like plot '1934', '1898/1934' also had the majority of its stags in the D≤40 cm classes, but it also had four stags with diameters 1.0 m or greater. Plot '1898' had few stags.

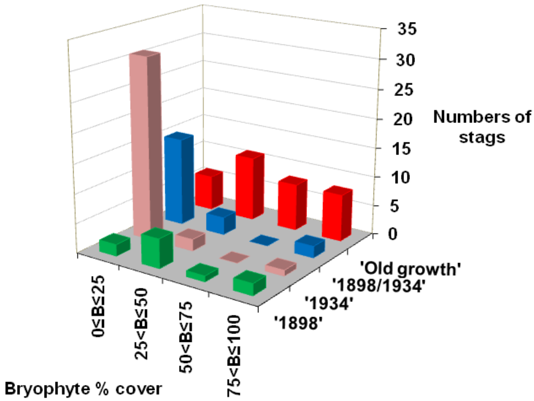

Figure 7. Stag numbers in bryophyte percentage cover classes. There is a stark contrast between the younger plots '1934' and '1898/1934', which had most of its bryophyte cover in the B≤25% class, and the more mature plots 'Old growth' and '1898', which have greater percentages of bryophytes in the higher cover classes.

Table 3. The total number of stags, number of *E. obliqua* stags, average stag diameter and total stag volume in the four plots.

		Plot		
	'Old growth'	**'1898'**	**'1934'**	**'1898/1934'**
Total no. of stags	33	10	34	20
No. of *E. obliqua* stags	1	1	16	12
Ave. stag diam., overall, cm	48.3	39.9	28.5	50.2
Ave. stag diam., eucalypts, cm	150	25	34.7	23.2
Volume of stags, m^3/ha	**226**	**47**	**192**	**176**

Volumes of CWD from other studies

Sohn (2007) measured the volumes of CWD in plots of the chronosequence study of Turner *et al.* (2007). Of interest here are the four plots having a southerly aspect, viz. '1966S', '1934S', '1898S' and 'OGS'. Although these plots were of size 50 x 50 m, as in the present study, Sohn (2007) used a lower diameter limit of 40 cm, thereby obtaining volumes that are somewhat lower than if a 10 cm lower diameter, as in the present study, had been used. The CWD volumes from these plots, corrected for their reduction in volume resulting from the use of a different lower diameter limit, is given in Table 4. Woldendorp *et al.* (2004) inventoried the CWD in two wildfire-affected plots in the tall wet *E. obliqua* forests of the Warra LTER, both having a southerly aspect and which were not amongst the four plots of the present study nor amongst the four plots of a southerly aspect measured

Table 4. Volumes of CWD from the plots of the present study, and from those of Woldendorp *et al.* (2004), Yee (2005), Sohn (2007) and Thauvin *et al.* (2010), all of which come from mature unlogged forests. Volumes include downed wood and stumps, but exclude stags.

Plot ID	Age, yr	CWD volume, m^3/ha	Source of data
'1966S'	41	408 (510)	Sohn (2007)
'TAS3'	58	744	Woldendorp *et al*. (2004)
'PO1'	67	876	Yee (2005)
'PO2'	67	769	Yee (2005)
'TAS2'	68	1236	Woldendorp *et al*. (2004)
'1898P'	72	1431	Present study
'1934'	72	1091	Present study
'1898/1934'	72	701	Present study
'1934S'	73	539 (674)	Sohn (2007)
'1898S'	73	360 (450)	Sohn (2007)
'WR'	87	847	Yee (2005)
'M'	95	938	Yee (2005)
'R'	95	633	Yee (2005)
'1898R'	108	1481	Present study
'Old growth'	>250	838	Present study
'OGS'	>250	869 (1086)	Sohn (2007)
Mature forest	—	560	Thauvin *et al*. (2010)

The plot '1898' of the present study is divided into its two component parts, viz. '1898P' for the subplots that predominantly contain *Pomaderris apetala* and '1898R' for the subplots that predominantly contain rainforest species. CWD volumes from Yee (2005) are divided by 0.25 to convert the values measured on 0.25 ha plots to a per hectare basis. Volumes from Sohn (2007) were measured on logs having a minimum diameter of 40 cm, whereas the other studies used a minimum diameter of 10 cm. This results in an underestimation of the CWD volume by an amount estimated by Sohn (2007) as ca. 25%. Therefore, values are also given (in parentheses) which predict what the CWD volumes might have been had a minimum 10 cm diameter been used. The CWD volume for mature forest from Thauvin *et al.* (2010) is the average of 28 plots (each 50 x 50 m) of varying ages; plots derived from silvicultural regeneration are not included.

by Sohn (2007). The size of these plots was 1 ha each, i.e. four times the size of each of the plots of the present study, and the definition of CWD was slightly different, having lower diameter and length limits of 15 cm and 50 cm, respectively (instead of the 10 cm diameter limit and the 1 m length limit used here). Because '1898' of the present study is really made up of two fire histories, it was split into two parts for inclusion in Table 4, with '1898P' based on subplots where *Pomaderris apetala* (common dogwood) was the predominant understorey species, and '1898R' based on subplots where rainforest species were predominant. Yee (2005), using a line transect method, measured dead wood volumes for ten 50 x 50 m plots, but as five of those plots were in regenerated sites after logging, only the five plots from mature unlogged forests are considered here. The CWD volumes from Yee (2005, Table 2.7) are included in Table 4 after dividing by 0.25 to convert the volumes that were based on her 0.25 ha plots to m^3/ha. The most recent and comprehensive study of CWD was that of Thauvin *et al.* (2010), who used 56 plots of size 50 x 50 m, 28 of which were in silviculturally regenerated sites and 28 of which were in mature forest. Only the latter are considered here and because they did not tabulate CWD volume as a function of individual plot age, only the overall mean CWD volume 560 m^3/ha is included in Table 4. This table clearly shows the large variation of CWD volume for plots of the same or closely similar ages, wherever ages are available, especially those of 72–73 years since wildfire.

Discussion

The sources of CWD for the four plots of the present study are (1) the stand prior to the disturbance, (2) the direct result of the disturbance itself, and (3) an ensuing gradual input from the current stand, including mortality caused by disease, suppression and competition, insect attack, and windthrow. Although located within ca. 1 km of each other, the four plots have different fire histories and therefore probably have different mechanisms by which the major part of their CWD was likely to have originated. In Tasmania, in the long absence of fire and in areas where the annual rainfall exceeds 1270 mm, ecological drift occurs (Jackson 1968). This means that the wet eucalypt forests progressively becomes mixed forest as their understorey is dominated by cool temperate rainforest and, as the eucalypts die without regeneration, the eventual outcome that may take ca. 400 years to occur is climax rainforest. The 'Old growth' plot fits the definition of mixed forest (old, even-aged eucalypts, with an understorey of mature rainforest; see Gilbert 1959 and Wells & Hickey 1999). The live vegetation showed floristic simplification with a preponderance of mature rainforest species and two very large surviving eucalypts (see Gates & Ratkowsky 2016). Only one stag in 'Old growth' was of *E. obliqua* origin, compared to 32 stags of rainforest and/ or other species (Table 3). Pieces of CWD in 'Old growth' had the highest percentage bryophyte cover of all the plots, a consequence of the direct relationship between decay class of the wood and percentage bryophyte cover (Figure 5). The most likely origin of the high percentage of pieces of CWD in high decay classes (Figure 4) and of small diameter (Figure 3) in 'Old growth' was from branches breaking out of declining eucalypt crowns and from the tops of stags from climax rainforest species falling to the forest floor. The sparseness of large diameter CWD in high decay classes in 'Old growth' suggests that sufficient time (>300 yr., Grove *et al.* 2009) had elapsed for the CWD resulting from the death and falling of the original mature eucalypt stand to rot away.

The '1898' plot was made up of two distinct vegetation types. The partition '1898R', an area characterised by living rainforest species, had a CWD volume of 1481 m^3/ha, due to some very large pieces of CWD of *E. obliqua* origin that may have resulted from trees killed by an intense and possibly stand-replacing fire in the year 1898. These trees likely fell immediately after the fire or subsequently as a result of wind or disease. Any small diameter branch wood or suppressed trees of small diameter from the regenerating stand could have had sufficient time (108 years) to rot away, which may explain the relatively low percentage of pieces of CWD in the 15<D≤30 cm diameter class (Figure 3).

However, the stand may not have been old enough for the accumulation of small diameter CWD of the rainforest species that were found in 'Old growth'. In this rainforest partition of '1898', there were three very old *N. cunninghamii* stags consistent with an old growth plot. The partition '1898P' had a CWD volume almost as high as for '1898R', also due to a few very large diameter trees, but in a significantly lower decay class (data not shown), consistent with fallen wood being on the forest floor for a shorter period of time.

In '1934', the lower average decay class of the CWD reflects the shorter time (72 years) that the wood has been lying on the forest floor. The high number of small diameter stags (Figure 6) may reflect suppression mortality in the regenerating stand. A striking difference between the composition of the living stems of '1934' and that of '1898/1934' and of '1898P', plots or parts of plots that experienced a second fire in 1934, is the presence of *Monotoca glauca* (goldey wood) and the absence of *Pomaderris apetala* (see Gates & Ratkowsky 2016). This can be attributed to a different underlying geology. Whereas the other plots are on soils derived from Jurassic dolerite, '1934' is situated on Permo-Triassic sedimentary rock, which produces a more acidic soil type that favours *Monotoca* in place of *Pomaderris* (Balmer 2016).

The '1898/1934' plot had the smallest volume of CWD (Table 2), which is consistent with the second fire consuming the CWD generated by the first fire. Alternatively, perhaps the large diameter trees that were killed by the fire of 1898 did not fall immediately but remained as stags, which survived the fire of 1934 (see Figure 6). Any small diameter stags that resulted from regeneration after the first fire and later suppressed by competition to become small diameter CWD on the forest floor, were likely to have been consumed by the second fire. Suppression mortality in the regenerating stand following the second fire was likely to have been responsible for the many small diameter stags of *E. obliqua* origin (Table 3), similar to '1934'.

CWD volume varies greatly among forest plots that are otherwise very similar in wildfire history. Discrepancies in CWD volumes of the order of magnitude observed in Table 4, with a range of 360–1431 m^3/ha for an age of 72–73 years, cannot be attributed to differences in the lower diameter limit. That is, if a lower diameter limit of 40 cm had been used in the present study instead of 10 cm, 92.3% of the total volume would still have been observed, as the total volume is determined mainly by large diameter logs. The amount of CWD in a 50 x 50 m plot $\geq$ 72 years old regenerating in these native forests is largely a matter of chance, the main contributors to CWD volume being fallen eucalypts, some of which had heights exceeding the 50 m plot length. A single fallen tree in a 50 x 50 m area can have a big effect on CWD volume, e.g. the largest piece of CWD in 'Old growth' (clearly visible on the right-hand side of Figure 2a) accounted for 42.1% of the CWD volume in that plot. There were other large old trees and stags outside the boundary of the plot that could have randomly fallen and landed in the plot. Therefore, the fact that CWD volumes vary greatly is not surprising. Another point to note is that if all the stags had fallen to become CWD, the rank orders of the total amount of dead wood in the plots would remain unchanged, as the stag volumes in a plot are only a fraction ($\leq$21%) of the CWD volumes. That is, '1898' would still be the plot with the most total dead wood, '1934' would remain second highest, 'Old growth' would remain next and '1898/1934' would still have the least total dead wood.

The great variability in CWD volume that can occur in stands of the same age in what is ostensibly the same forest type is an impediment to the development of a stand dynamics model, that is, one that attempts to predict the long-term effects of stand-replacing fires or disturbances such as logging and fuelwood harvesting. One such model is that of Grove & Stamm (2011), who explored six disturbance scenarios, four of which were wildfire scenarios, in the same tall, wet eucalypt forest as in the present study. That deterministic model explored the effect of repeated replacement cycles over a period of 1200 years on the volume and mass of downed woody debris (DWD), of which CWD is a subset. Testing the validity of that or other simulation models using real data requires a great deal of replication, especially in view of the variability in woody debris volume that occurs in this forest type. Another impediment is the lack of a precise age for the 'Old growth' plot of the present study and the 'OGS' plot of the Turner *et al.* (2007) study, which poses difficulties for the development of a regression model. There is also a conspicuous absence of data for stand ages between 108 years and the age of the old growth stands. The experimental procedure of Sohn (2007) (see also Sohn *et al.* 2013), which used a minimum CWD diameter of 40 cm (rather than the 10 cm minimum employed in the present study) and the line transect sampling method (rather than measuring the dimensions of each piece of fallen wood) facilitated the determination of CWD volumes, thereby reducing the time it takes to survey a 50 x 50 m plot. Future studies, adopting such time-saving approaches, could provide the quantitative values for the CWD volumes in these forests that are required to test stand dynamics models and help make decisions about the management of Tasmanian wet forests with a view towards sustainability. The challenge may be to develop energy-efficient methods so that the maintenance of mixed forests is done in a manner that minimises the overall expenditure of energy, makes a minimal contribution to global warming, and maintains carbon neutrality. Tackling this challenge, and solving it, should enable Tasmania to have a viable forest industry whilst avoiding the experience of Fennoscandia, where forests denuded of CWD led to numerous life forms becoming extinct or being "red-listed". Understanding the role that CWD plays in the Tasmanian ecosystem is the key to enlightened management.

Acknowledgements

Financial and logistic support for the field work was provided by Forestry Tasmania. One of the authors (GMG) received financial support from an Australian Postgraduate Award, the Holsworth Wildlife Endowment Fund, the Cooperative Research Centre (CRC) for Forestry, the Bushfire CRC, and CSIRO Ecosystem Sciences. Additional logistic support was provided by the then School of Agricultural Science and the then School of Plant Science of the University of Tasmania, now the School of Land & Food and the School of Biological Sciences, respectively. We gratefully acknowledge the helpful suggestions and additional references provided by Dr. Marie Yee.

References

Alcorn, P.J., Dingle, J.K. & Hickey, J.E. (2001). Age and stand structure in a multi-aged wet eucalypt forest at the Warra silvicultural systems trial. *Tasforests* 13: 245–259.

Ashton, D.H. (1981). Fire in tall open-forests (wet sclerophyll forests). In: *Fire and the Australian Biota* (eds. A.M. Gill, R.H. Groves & I.R. Noble), pp. 339–366, Australian Academy of Science, Canberra.

Balmer, J. (2016). Floristic response to landscape context in vascular plant communities in *Eucalyptus obliqua* and *Eucalyptus regnans* wet forest, southern Tasmania. Ph.D. Thesis, University of Tasmania. (http://eprints.utas.edu.au/23020/1/Balmer_whole_thesis.pdf).

Cline, S.P., Berg, A.B. & Wight, H.M. (1980). Snag characteristics and dynamics in Douglas-fir forests, Western Oregon. *Journal of Wildlife Management* 44: 773–786.

Gates, G.M., Mohammed, C., Wardlaw, T., Ratkowsky, D.A. & Davidson, N.J. (2011). The ecology and diversity of wood-inhabiting macrofungi in a native *Eucalyptus obliqua* forest of southern Tasmania, Australia. *Fungal Ecology* 4: 56–67. http://dx.doi.org/10.1016/j.funeco.2010.07.005

Gates, G.M. & Ratkowsky, D.A. (2016) Seeing the forest for the trees – floristic composition in a tall, wet *Eucalyptus obliqua* forest of southern Tasmania. *Tasmanian Naturalist* 138: 21–28.

Gilbert, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 93: 129–151.

Gill, A.M. (1997). Eucalypts and fires: interdependent or independent? In: *Eucalypt Ecology: Individuals to Ecosystems* (eds. J. Williams & J. Woinarski), pp. 151–167, Cambridge University Press, Cambridge.

Grove, S. (2009a). A decade of deadwoodology at Warra. *Tasmanian Naturalist* 131: 25–35.

Grove, S.J. (2009b). Beetles and fuelwood harvesting: a retrospective study from Tasmania's southern forests. *Tasforests* 18: 77–99.

Grove, S., Meggs, J. & Goodwin, A. (2002). *A Review of Biodiversity Conservation Issues Relating to Coarse Woody Debris Management in the Wet Eucalypt Production Forests of Tasmania.* Forestry Tasmania, Hobart.

Grove, S.J. & Stamm, L. (2011). *Downed woody debris in Tasmanian eucalypt forest: modelling the effects of stand-replacing disturbance dynamics.* Division of Forest Research and Development, Technical Report 15/2011, Forestry Tasmania, Hobart.

Grove, S.J., Stamm, L. & Barry, C. (2009). Log decomposition rates in Tasmanian *Eucalyptus obliqua* determined using an indirect chronosequence approach. *Forest Ecology and Management* 258: 389–397.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K. & Cummins, K.W. (1986). Ecology of coarse woody debris in temperate ecosystems. In: *Advances in Ecological Research,* Vol. 15 (eds. A. MacFadyen & E.D. Ford), pp. 133–302. Academic Press, New York.

Harmon, M.E. & Sexton, J. (1996). *Guidelines for Measurements of Woody Detritus in Forest Ecosystems.* Publication No. 20, U.S. Long-Term Ecological Research Network Office, University of Washington, Seattle.

Jackson, W.D. (1968). Fire, air, water and earth – an elemental ecology of Tasmania. *Proceedings of the Ecological Society of Australia* 3: 9–16.

Jonsson, B.G. (2000). Availability of coarse woody debris in a boreal old-growth Picea abies forest. *Journal of Vegetation Science* 11: 51–56.

Kirkpatrick, J.B. & Backhouse, S. (1981). *Native Trees of Tasmania*. Pandani Press, Hobart.

Lindenmayer, D.B., Claridge, A.W., Gilmore, A.M., Michael, D. & Lindenmayer, B.D. (2002). The ecological roles of logs in Australian forests and the potential impacts of harvesting intensification on log-using biota. *Pacific Conservation Biology* 8: 121–140.

Luke, R.H. & McArthur, A.G. (1978). *Bushfires in Australia*. Australian Government Publishing Service, Canberra.

McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005). Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management* 218: 1–24.

Moroni, M.T., Musk, R. & Wardlaw, T.J. (2017). Forest succession where trees become smaller and wood carbon stocks reduce. *Forest Ecology and Management* 393: 74–80.

Motta, R., Berretti, R., Lingua, E. & Piussi, P. (2006). Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. *Forest Ecology and Management* 235: 155–163.

Pyle, C. & Brown, M.M. (1999). Heterogeneity of wood decay classes within hardwood logs. *Forest Ecology and Management* 114: 253–259.

Sohn, J.A. (2007). Variation in coarse woody debris attributes in Tasmanian tall wet *Eucalyptus obliqua* (L'Herit.) forests and implications for its monitoring. Diplomarbeit, Waldbau Institut, Albert-Ludwigs-Universität, Freiburg.

Sohn, J., McElhinny, C., Grove, S., Hilbig, E. & Bauhus, J. (2013). A simplified inventory approach for estimating carbon in coarse woody debris in high-biomass forests. *Papers and Proceedings of the Royal Society of Tasmania* 147: 15–23.

Spies, T.A., Franklin, J.F. & Thomas, T.B. (1988). Coarse woody debris in Douglas-Fir forests of Western Oregon and Washington. *Ecology* 69: 1689–1702.

Stokland, J.N. & Sippola, A.-L. (2004). *Monitoring protocol for wood-inhabiting fungi in the Alberta Biodiversity Monitoring Program*. Alberta Biodiversity Monitoring Program, Version 2.9.

Thauvin, G., Libis, E., Grove, S.J. & Wardlaw, T. (2010). *Comparison of coarse woody debris volumes between mature and silviculturally regenerated eucalypt forest along a disturbance gradient*. Technical Report 15/2010, Forestry Tasmania, Hobart.

Turner, P., Airey, C. & Grove, S. J. (2007). *Wildfire chronosequence project establishment report*. Forestry Tasmania, Division of Forest Research and Development.

Turner, P.A.M., Balmer, J. & Kirkpatrick, J.B. (2009). Stand replacing wildfire? The incidence of multi-aged and even-aged *Eucalyptus regnans* and *E. obliqua* forests in southern Tasmania. *Forest Ecology and Management* 258: 366–375.

Wardlaw, T., Grove, S., Hopkins, A., Yee, M., Harrison, K. & Mohammed, C. (2009). The uniqueness of habitats in old eucalypts: contrasting wood-decay fungi and saproxylic beetles of young and old eucalypts. *Tasforests* 18: 17–32.

Wells, P. & Hickey J. (1999). Wet sclerophyll, mixed and swamp forest. In: *Vegetation of Tasmania* (eds. J.B. Reid, R.S. Hill, M.J. Brown & M.J. Hovenden), pp. 224–243, Australian Biological Resources Study, Canberra.

Woldendorp, G. & Keenan, R.J. (2005). Coarse woody debris in Australian forest ecosystems: A review. *Austral Ecology* 30: 834–843.

Woldendorp, G., Keenan, R.J., Barry, S. & Spencer, R.D. (2004). Analysis of sampling methods for coarse woody debris. *Forest Ecology and Management* 198: 133–148.

Wu, J.-B., Guan, D.-X., Han, S.-J., Zhang, M. & Jin C.-J. (2005). Ecological functions of coarse woody debris in forest ecosystem. *Journal of Forest Research* 16: 247–252.

Yee, M. (2005). *The ecology and habitat requirements of saproxylic beetles native to Tasmanian wet eucalypt forests: potential impacts of commercial forestry practices.* Ph.D. Thesis, University of Tasmania, School of Agricultural Science, Hobart.

Yee, M., Yuan, Z.-Q. & Mohammed, C. (2001). Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. *Tasforests* 13: 119–128.